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High air temperatures induce temporal, spatial and social changes in the foraging behaviour of wild zebra finches

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Understanding how heatwaves affect organisms is becoming an important issue in animal behaviour, given the changing climate. Exposure to high air temperatures can lead to lethal hyperthermia, when individuals are no longer able to maintain body temperature within their optimal physiological range. Animals will rapidly adjust their behaviour, prioritizing heat dissipation through activities such as drinking and sitting in shade to maintain their body temperature over other activities, such as foraging. Here, we used an automated logging system to consider both the spatial and temporal foraging patterns under a range of different air

temperatures at an individual level, in a strictly granivorous species in the wild. We continuously monitored individual foraging activity of wild zebra finches, *Taeniopygia guttata*, a species well adapted to arid conditions, in an Australian arid area across two heatwave events. High air temperatures significantly reduced foraging activity, with the extent of this effect depending on the time of day. They also led to a significant decrease in the number of birds foraging together and to birds spending a higher proportion of their foraging activity close to a water supply. As temperatures exceeded 35 °C we saw a significant escalation of heat dissipation behaviour. Our results indicate that extreme air temperatures significantly affected temporal, social and spatial characteristics of zebra finch foraging behaviour and these are likely to adversely reduce an individual's capacity to forage efficiently, and consequently its food intake in the short term, while also potentially having implications for both reproduction and survival in the long term.

Keywords: arid environment, climate change, foraging, heatwave, heat dissipation behaviour, *Taeniopygia guttata*

Understanding how heatwaves affect organisms and ecosystem dynamics is becoming an important question in animal ecology (Ummenhofer & Meehl, 2017). Short-term behavioural decisions and patterns of behaviour are affected by heat (e.g. Levy, Dayan, Porter, & Kronfeld-Schor, 2016), and repeated or prolonged exposure to elevated temperature has been demonstrated to have adverse and often long-lasting consequences on both endotherms and ectotherms (reviewed in: Khaliq et al. 2004, Grant et al. 2017). Exposure to extreme temperatures can lead to lethal hyperthermia, which occurs when an individual is not able to lose heat faster than it is taken on or produced metabolically (Boyles, Seebacher, Smit, &

McKechnie, 2011). Endotherms vary in their heat tolerance, but high tolerances may lead to energetic and physiological costs (Boyles et al., 2011; Jiguet et al., 2006). Small and diurnal animals are particularly affected by repeated exposure to sublethal temperatures (Gardner, Amano, Sutherland, Clayton, & Peters, 2016; McKechnie & Wolf, 2010). Endothermic animals react to high temperatures by adjusting their behaviour (e.g. reducing activity, seeking shade) and physiology (e.g. evaporative cooling, vasodilatation) to maintain their body temperature (Wingfield et al., 2017). At a critical air temperature threshold, many mammal and bird species rapidly adjust their behaviour to prioritize heat dissipation behaviour over other behaviours, such as foraging and parental care (du Plessis, Martin, Hockey, & Susan, 2012; Edwards, Mitchell, & Ridley, 2015; Levy et al., 2016). In birds, previous studies on thermoregulation and related trade-offs have been based on short and discontinuous focal observations, limited in time and sample size (Carmi-Winkler, Degen, & Pinshow, 1987; du Plessis et al., 2012; Edwards et al., 2015; Smit, Harding, Hockey, & McKechnie, 2013; Tieleman & Williams, 2002). Furthermore, while previous studies (cited above) have focused on time budgets spent on foraging and the efficiency of foraging in different conditions in insectivorous and territorial species, there has been no examination of granivorous and nonterritorial species and their spatial pattern of movement in hot weather. We may expect very different findings because the former are spatially constrained by their territory, and typically do not drink free-standing water, while the latter are less constrained spatially, and often consume free-standing water regularly, particularly to help alleviate the effects of heat (Smit, Woodborne, Wolf, & McKechnie, 2018). Small birds have limited capacity for water storage and a high metabolic rate with high internal heat production (reviewed in Wolf 2000), with water often being used in evaporative cooling to prevent overheating (Calder, 1964; Calder & King, 1963; Tieleman & Williams, 1999). Therefore, the increasing value of water to small birds as temperatures rise should impose constraints on

movement. Specifically, in an arid environment during hot conditions, those granivorous species that depend on water for cooling will face a trade-off between the need to be near a water source and the need to forage in other areas, since the vegetation composition changes around artificial water with a decreased abundance of grass species and increase of woodlands and shrublands (James, Landsberg, & Morton, 1999). It is revealing that in the cases of significant avian mortality reported in arid-adapted species, the dead birds were found near water (McKechnie, Hockey, & Wolf, 2012; McKechnie & Wolf, 2010).

While these mortality events are rare, repeated exposure to sublethal hot temperatures affects individual fitness in both the short and the long term (du Plessis et al., 2012). A recent analysis of 37 years of data found evidence for carryover physiological costs of short events of extreme conditions in summer and winter that decreased annual survivorship in two Australian passerine species (Gardner, Rowley, de Rebeira, de Rebeira, & Brouwer, 2017). Investigating the relative plasticity of physiological and behavioural traits during short and unpredictable environmental changes ('perturbation resistance potential') can help to define when a change should be considered extreme, indicate how the availability of energetic resources will be affected and predict the degree to which a population will be able to resist projected climates in the future (Wingfield et al., 2017). Extreme temperatures are also likely to compromise reproduction through a number of pathways: a recent analysis on the breeding phenology of over 300 Australian bird species found that, in the hot arid areas of inland Australia, birds typically avoid breeding in the summer months, presumably to avoid the extreme heat during this time (Duursma, Gallagher, & Griffith, 2017). Reproduction may be compromised by the effect of hot weather on reproductive physiology, such as damage to sperm (e.g. Hurley et al. 2018), but even if reproduction is successful, in hotter conditions the size and mass of offspring are reduced (e.g. Cunningham et al. 2013, Gardner et al. 2016, Andrew et al. 2017, 2018).

Although the production of smaller offspring in hot conditions (e.g. Andrew et al., 2017) could be a direct physiological effect of the heat on offspring development, it may also be caused by constrained levels of parental care during extremely hot ambient conditions. To test the idea that foraging ability may be constrained by extreme heat, we monitored the foraging behaviour of individual zebra finches, *Taeniopygia guttata*, in the Australian arid zone during summer, monitoring them at fine timescales over several weeks and across the whole study area. The aim was to investigate how temperature fluctuations influenced hour-by-hour individual patterns of foraging behaviour across two separate heatwaves. Importantly, our approach also permitted the analysis of the spatial distribution of individual foraging behaviour in relation to a water source across a range of air temperatures. Given the importance of water to thermoregulation in the zebra finch (Calder, 1964), we predicted that zebra finches would forage closer to the water source in the hottest conditions to remain close to this important resource. In contrast, when the temperature was not as extreme, the zebra finches were expected to forage more evenly across the landscape, since their natural foraging patches are often further from artificial water sources (James et al., 1999). At the same time, we also conducted an observational study on zebra finch behaviour, relating it with air temperature, to provide some additional context with respect to the point at which birds initiate heat dissipation behaviours.

<H1>Methods

<H2>Study species

The zebra finch is a small (10 cm, 9–15 g), sexually dimorphic passerine, abundant and widespread across inland Australia. It is strictly granivorous, highly gregarious and described as both resident and nomadic depending on the resources available (Zann, 1996). The study

was conducted in Gap Hills (30°56.96'S, 141°46.01'E), an area of approximately 2 km^2, at Fowlers Gap Arid Zone Research Station, New South Wales, Australia. The area is composed of a large patch of scattered shrubs (*Acacia* spp.), around a permanent dam (200x150 m) and associated with a mostly dry ephemeral creek system (Mariette & Griffith, 2012). Here, 230 nestboxes allow the monitoring of zebra finches' reproduction in a long-term study (Griffith, Pryke, & Mariette, 2008). By the beginning of the current study in January 2017, a total of 158 adult birds were caught using mist-net, feeders and nestboxes' traps, banded and tagged subcutaneously with passive integrated transponder (PIT) tags (Minichip; Micro Products Australia, Perth, Australia), allowing us to assay their foraging behaviour at monitored feeders as described below.

<H2>Foraging behaviour

Foraging behaviour was measured using artificial feeders at the end of the breeding season, between January and February 2017, when the temperatures are typically hottest, that is, we were studying the birds in a period of the year when recent work suggests that they are less likely to breed because of the heat (Duursma et al., 2017). Feeders were placed randomly within a radius of approximately 800 m of the dam (Fig. 1a), which was the only source of drinking water for the birds within at least 5 km. Each feeder was at least 50 m from the nearest nestboxes and the dam, at least 2 m from the closest vegetation and with the entrance facing a tree or bush. Feeders consisted of a mesh cage (70x40 cm and 50 cm high), partially buried in the ground and open on one side, where the birds could enter the feeder by passing through an antenna (11 cm in diameter). The antenna was linked to a PIT tag reader (RFIDRW-E-232; Priority 1 Design, Melbourne, Australia) and a battery (6 V) that recorded every time a tagged

145 bird passed through the antenna, its unique ID code, the date and time. During the study all the
146 feeders (two trials of 16) were equipped with an antenna and PIT tag reader.

147 We established 16 feeders on 15 January 2017 (first trial). Feeders were initially
148 provisioned with 120 g of commercial finch seed mixture. After 9 days (i.e. on 24 January) the
149 positions of the 16 feeders were changed (second trial) and they remained there for another 13
150 days until 7 February. Every 2 days the batteries of the PIT tag readers were changed, and any
151 uneaten seed (commercial finch mix) or seed husks were removed and replaced by 60 g of new
152 seeds. Therefore, feeders were consistently and regularly replenished so that the quantity of
153 food provided was equally distributed across them, once monitoring began. We collected 62
154 306 data records from 158 individual zebra finches foraging in two trials of 16 feeders (32
155 feeders in total) across 3 weeks. From the reader data, it was not possible to infer the direction
156 of movement through the antenna, but, as previously validated (Mariette et al., 2011), we used
157 a 15 min rule, whereby any two readings within 15 min were assumed to be the same visit to a
158 feeder. We only considered data from adults that visited feeders in both trials and at least 10
159 times per trial, to exclude individuals that rarely visited the feeders, reducing the sample size
160 to 81 birds. We excluded the days on which the feeders were set up for the first time (15
161 January), when the feeders were moved for the second trial (24 January) and removed (7
162 February). Finally, we also excluded the first 4 days of the first trial (16–19 January), when
163 birds were becoming habituated to the feeders and numbers were low (McCowan, Mainwaring,
164 Prior, & Griffith, 2015), whereas the sample size remained constant throughout the whole of
165 trial 2. Thus, we analysed data from 17 days with varying air temperature conditions (illustrated
166 in Fig. 1b).

167

168 *<H2>Behavioural observations on heat stress*

Between 17 January and 26 February 2017, we made behavioural observations to evaluate heat stress at a nearby site, 6.9 km from the Gap Hills dam, known as 'White Tank' (31°00.53'S, 141°47.36'E). This work was conducted at this site so as not to disturb the birds' normal behaviour at Gap Hills during the monitoring study described above. To assess heat-related behaviour in adults, we set up a video camera directed to a small section of a fence (1.5 m wide) located in direct sunlight within a couple of metres from a small but permanent artificial water source (a trough for stock). We analysed individual behaviour during videos of 30 min periods. Although these birds were not individually marked, we recorded any individual perching on the fence as an 'observation'. Observations ranged from a fraction of a second to 316 s, but visits shorter than 5 s were discarded as we were interested in behaviour in a resting state rather than in a very brief stop between two flights (after discarding <5 s visits: mean 'resting state' observation duration ± SD = 19.3 ± 20.4 s, $N_{\text{observations}}$ = 1454). After removing two recording periods where no birds visited our focal site, our data consisted of 20 half-hour periods recorded on 19 different days (i.e. one to two periods per day), with the earliest zebra finch visit (observation) made at 0815 and the latest at 1644 hours and the rest relatively evenly spaced over the course of the day. From the videos, during each observation (visit at the water source) we recorded as responses to heat the proportion of time an individual (1) kept its bill open (gasping when breathing, Zann, 1996), (2) held its wings away from its body (lifting the shoulder away from the body to facilitate air flow over the underwing, Zann 1996), (3) exhibited a 'spread out' position when both the wings and the tail were spread and (4) kept its tail fanned when not in a 'spread out' position.

<H2>Temperature data

We obtained continuous air temperature data (accuracy: 1 min) recorded at the Australian Bureau of Meteorology automated weather station (AWS) based close to the Fowlers Gap homestead, and 16.9 km from Gap Hills and 12.4 km from 'White Tank'. Since the study locations and the weather station are at similar elevations (Gap Hills: 155.9 m; White Tank: 147.9 m; Fowlers Gap AWS: 181.0 m), and relatively close, we assumed that the temperature recorded here would closely reflect those at the two study sites. Based on long-term climatic data at our field site, we considered a heatwave to be any period when the daily maximum atmospheric temperature exceeded 40 °C on 2 or more consecutive days (Hurley et al., 2018).

<H2>Ethical note

The work was approved by the Macquarie University Animal Ethics Committee (Animal Research Authority 2015/017) and the Australian Bird and Bat Banding Scheme.

<H2>Data Analysis

<H3>Hour by hour temperature and foraging

The detailed temperature data were processed to obtain the average temperature per hour during the recorded zebra finch foraging activity (0600–1959 hours) for all subsequent analyses. A linear mixed-effect model with normal error structure (LMM) was performed to test the relationship between temperature and the hour of the day during the study period. The average temperature per hour was fitted as the dependent variable, the hour of the day as a fixed term and the date as a random term. Using the maximum threshold of 15 min to define independent feeder visits and having reduced the data set as described, we summarized individual foraging activity on an hourly basis as a binary variable (yes/no; feeding occurred/did not occur within

a given hour). To understand the relationship between individual foraging behaviour, temperature and time of day, we built a generalized linear mixed model (GLMM) with binominal error distribution and we fitted the binary foraging activity (yes/no) variable as the dependent variable and average temperature per hour, time of day (hour) and their interaction as fixed terms. We included the time of day in the model to account for variables that we did not directly measure but are likely to be related to the time of day and may influence foraging, including both extrinsic (e.g. changes in shade) and intrinsic variables (e.g. diurnal patterns of physiology and nutritional state). Individual ID and date were set as random terms.

Foraging behaviour may be considered a two-step process (Levy et al., 2016), whereby as well as deciding whether or not to forage during a particular period of the day, individuals can also vary the duration of bouts of foraging. To test for the influence of air temperature on the duration of foraging activity, we examined the number of 5 min intervals in which an individual was recorded at each feeder it visited as a proxy for foraging duration. We took this approach because the decoders on the feeders do not record entry and exit of individuals (Mariette et al., 2011; see above). We built a GLMM with Poisson error structure to investigate the probability that an individual was recorded at any feeder during each 5 min period (number of periods summed per hour; i.e. values from 1 to 12 possible), to reflect what proportion of the day each individual was out actively foraging. This foraging duration proxy was the dependent variable, average air temperature per hour, time of day (hour) and their interaction were fixed terms and individual ID, feeder ID and date were random terms.

We also analysed the first and last feeding event per day, as minutes since sunrise and minutes since sunset, respectively. First, we excluded the visits that represent the two tails of the distribution with respect to early and late visits to the feeders, to remove birds that did not visit the feeders at all early in the morning or late in the afternoon. The threshold of exclusion was determined by plotting the bimodal distributions of the first and last feeding events, and

removing the outliers from the interquartile range above the third quartile (i.e. first foraging 2 h after sunrise), eliminating 10.6% of first feeding events, and from the interquartile range below the first quartile (i.e. last foraging 3.5 h before sunset), excluding 8.4% of last feeding events. Then, we tested whether the first and last feeding events (in relation to sunrise and sunset) were linked to the temperature at sunrise and sunset, respectively. We ran an LMM with time of first feeding event as the dependent variable, temperature at sunrise as a fixed term and individual ID and date as random terms. The same model was run for the last foraging event and the temperature at sunset.

<H2>Temperature and foraging site to water distance

To test the relationship between temperature and foraging activity in relation to the water source (a dam), we calculated the distance to the dam of each feeder visited and built an LMM with this distance as the dependent variable, average temperature per hour, time of day and their interaction as fixed terms and individual ID, feeder ID and date as random terms. To further investigate the effect of air temperature on the zebra finches' spatial distribution in relation to the water source, we first identified the furthest feeders based on their distribution in relation to the dam (average distance to the water ± SD: furthest feeders = 732 ± 52 m, N = 6 x 2 trials; other feeders = 406.7 ± 140.5 m, N = 10 x 2 trials); then, we calculated the proportion of visits to the furthest feeders over the total number of visits per hour. Since the total number of visits changed with time of day (see Results), we excluded the hours with fewer than 10 visits (excluding 35 data points from the total of 237). A GLMM with binomial error structure was built with the proportion of visits to the furthest feeders as the dependent variable, average air temperature per hour, hour of the day and their interaction as fixed terms and date as a random term.

As conditions become hot, individuals may also change the locations at which they feed, placing greater reliance on a single feeder rather than travelling more widely to multiple feeders. Therefore, we built a model on the effect of air temperature on zebra finches' tendency to revisit the same feeder, rather than changing feeders. We calculated the proportion of visits by an individual to its most visited feeder per hour. Thus, we created an index of feeder fidelity that ranged from 0 to 1, with 1 indicating that an individual made all its visits within the given hour to one feeder, and values less than one, indicating that an individual used multiple feeders. A GLMM with binomial error structure was run: the feeder fidelity was fitted as the dependent variable, average air temperature per hour, time of day (hour) and their interaction as fixed terms and individual ID and date as random terms.

We also tested the effect of air temperature on social foraging, by counting zebra finches active at each feeder within 15 min intervals (when at least one zebra finch was present in this period). We built a GLMM with Poisson error structure and the number of birds per feeder during 15 min intervals was set as the dependent variable, average air temperature per hour as a fixed term and feeder ID and unique 15 min periods as random terms.

<H2>Temperature and heat amelioration behaviour

To test for a link between temperature and heat amelioration behaviour at 'White Tank' we transformed the data from proportion of time to presence/absence (binomial) of each behaviour per bird observation. For each behaviour we conducted one GLMM with a binomial distribution. The dependent variable was the presence/absence of each behaviour, fixed terms were temperature (average per hour), hour of the day and their interaction and the duration of observation (s) and date were included as random terms.

<H1>Results

Air temperatures (T_a) ranged between 17 °C and 44 °C during the study period (17 days: 4 days during trial 1 and 13 days during trial 2) and the hours of zebra finch feeder activity (between 0600 and 1959 hours). Temperature generally increased during the day (Table 1). Across the time of monitoring there were two heatwave events: from 29 to 31 January maximum daily temperature was 42–43 °C and from 4 to 6 February it ranged between 40.5 and 44 °C (Fig. 1b).

A total of 8484 feeder visits by the focal 81 tagged zebra finches (40 females and 41 males) were recorded. The likelihood that an individual was recorded foraging in a particular hour was predicted by temperature, and this depended on the time of day ($N_{observations}$=22 032 including the absences of an individual at a respective feeder; Fig. 2, Table 1). At air temperatures of 17 °C the predicted probability that an individual was foraging in each hour (across the hours of daylight) ranged between 55.6% and 56.7%, while at temperatures of 40 °C the foraging probabilities were much lower with a predicted range between 23.4% and 29.4%. Foraging activity was generally lower later in the day with the lowest predicted values (21–26%) at the highest temperatures (Fig. 2). With increasing air temperature, the foraging duration proxy (the sum of presence during 15 min intervals at a feeder per hour) decreased ($N_{observations}$=8385), independently of time of day and its interaction with temperature (Table 1).

The majority (89.4%) of the tagged individuals foraged for the first time each day between 26 min before sunrise and 2 h after sunrise. The time of the first foraging event, relative to the time of sunrise, was not influenced by temperature at sunrise ($N_{observations}$=1201; Fig. 3a, Table 1). The time of an individual's last foraging event ranged mostly (91.6%) between 3.5 h before sunset and 10 min after sunset. Birds visited the feeders for the last time 2.2 min later in the day with every increase of 1C at sunset ($N_{observations}$=1232; Fig. 3b, Table 1).

313 Overall, as air temperatures increased, zebra finches were more active at the feeders
314 closer to the dam ($N_{observations}$=8484; Table 1), independently of the time of day and the
315 interaction between time of day and temperature (Table 1). Specifically, the proportion of visits
316 to the feeders furthest to the dam decreased with increasing air temperature ($N_{observations}$=202;
317 Fig. 4). The predicted proportion of visits to these feeders decreased 0.31–0.98% per 1 °C of
318 air temperature, over the birds' activity period during the day. The time of day had an
319 independent positive effect on the proportion of visits to the furthest feeders from the dam
320 (Table 1).
321 The tendency of an individual to forage at the same feeder, measured as feeder fidelity,
322 increased with rising air temperature ($N_{observations}$=7032; Table 1, Fig. A1) but was independent
323 of the time of day and the interaction between temperature and time of day (Table 1). We also
324 found that the number of birds detected at an individual feeder (i.e. foraging together), within
325 each 15 min interval, was affected by the temperature (Table 1, Fig. 5) decreasing by 50%
326 between 18 and 41 °C.
327 The majority (73.5%, $N_{observations}$= 1454) of the bird observations on videos occurred
328 between 1100 and 1459 hours at 'White Tank'. The likelihood of the behaviour 'bill kept open'
329 increased with the interaction between temperature and hour of the day (Fig. 6a) and the
330 duration of the observation (Table 1). The behaviour 'wings held away from the body'
331 increased with temperature (Fig. 6b) and duration of the observation (1454), whereas it
332 decreased with the hour of the day (Table 1). The likelihood of the behaviour 'tail kept fanned'
333 and the 'spread out' position, with both tail and wing feathers spread, increased with increasing
334 air temperature (Fig. 6c, d) and with the duration of the observation (Table 1). The proportion
335 of time individuals held their bills open remained low until a slight increase at around T_a=33
336 °C, followed by a steep increase at 35 °C and a steady increase up until the highest temperatures
337 at 41–43 °C (Fig. 6a). Similar increases were noted with 'wings' at 35 °C and 'tails' at 39 °C

(Fig. 6b). The likelihood of individuals keeping their bills open peaked at 87.9% at 41–42 °C, 'wings' at 10.7% at 38–39 °C, 'tails' at 17.6% at 42–43 °C and 'spread out' at 12.7% at 41–42 °C (Fig. 6).

<H1>Discussion

We analysed the hour-by-hour foraging activity of 81 zebra finches over 17 days across a period of extreme hot weather, in an arid area in Australia, during which 12 days had maximum temperatures over 35 °C, and there were two heatwaves, with at least 2 consecutive days over 40 °C. We found that increasing air temperature led to a significant reduction in the amount of overall foraging that was observed across the population and in the proportion of time that individuals spent actively foraging. As well as reducing their foraging activity, birds foraged closer to the dam during hot weather. The intensive nature of our monitoring also allowed us to demonstrate a shift in the temporal distribution of foraging behaviour on hot days, with a higher level of foraging closer to dusk, presumably as birds were constrained by the heat from foraging earlier in the day. Both the increasing degree of feeder fidelity and the reduction in the duration of foraging each hour with increasing temperature suggested that the patterns of foraging that we have demonstrated both temporally and spatially were driven by the physiological constraints of foraging in hot conditions and the need to keep cool. This interpretation was also supported by the observed increase in heat dissipation behaviour with increasing temperature. A final important consequence of changes in foraging patterns during hot conditions was that birds foraged in smaller groups as temperature increased, and this may have important consequences for predation, if group foraging helps to reduce the risk of predation in this environment (e.g. Sorato, Gullett, Griffith, & Russell, 2012).

A negative effect of temperature on bird physiology and behaviour during the hottest parts of the day has been found in other studies, especially in arid environments (Smit et al., 2013; Tieleman & Williams, 2002). The need to prioritize thermoregulation has been shown to be the main constraint in foraging efficiency in a variety of species in extreme temperatures (Carmi-Winkler et al., 1987; du Plessis et al., 2012; Edwards et al., 2015; Smit et al., 2013; Tieleman & Williams, 2002). However, while our results are consistent with these earlier findings, our temporal and spatial data are more complete and provide important new insights into the relationship between heat and foraging. All these previous studies gathered data as short and discontinuous focal observations of individuals or groups (e.g. 20 min to 2 h per individual), and focused on insectivorous and territorial species, with relatively small numbers of individuals. While this kind of data certainly provides a good estimate of both the level of foraging activity and even foraging efficiency (du Plessis et al., 2012), across different temperatures, none of these earlier studies were able to consider individuals in a temporally complete way. The present study, by using PIT tag system, provided a more comprehensive overview of the effect of high temperature on foraging activity, following a greater number of individuals, consistently, during the entire daily activity range and over several weeks. Although the use of PIT tag technology has been used previously to explore foraging activity related to heat in a small mammal (Levy et al., 2016), our study provides the first evidence for a nonterritorial bird species facing an energetic trade-off between the need to stay near water and foraging activity, affecting both temporal and spatial daily patterns of behaviour.

Two important new insights emerged from our more intensive collection of data. First, we found that in addition to being constrained in the amount of foraging activity that was undertaken on hot days, the birds also had a spatially more constrained pattern of foraging behaviour. Different nutritional regimes are expected to reflect differences in resource allocation in trade-off balances (Flatt & Heyland, 2011; Ng'oma, Perinchery, & King, 2017),

such as that between thermoregulation and foraging behaviour. A recent study examined the difference in the drinking water needs of insectivorous, omnivorous and granivorous species of bird, highlighting the water dependence of the latter compared to other arid avifauna (Smit et al., 2018). While insectivorous and omnivorous species may be less reliant on water during hot periods, it would be interesting to examine the extent to which their movement behaviour changes in response to high temperature. Even though such species will not be constrained by the availability and location of surface water, they will presumably be constrained by the physiological need to reduce activity and the production of metabolic heat, as well as seeking shade and engaging in heat amelioration activity.

We found that individuals' activity increased at feeders closer to the dam (i.e. a source of drinking water) and reduced at the furthest feeders with increasing temperature, independently of the time of day. In our study, food was of the same quality across the range of feeders provided, and birds could therefore access a similar level of resources close to the dam. However, in natural circumstances it is likely that this restricted foraging range would impact their ability to find food efficiently, especially because natural foraging patches are generally further from artificial water sources, where the effect of selective grazing favours shrubland over grasslands (James et al., 1999). Given the similar quality and quantity of food in the different feeders, the shift in pattern relative to the water source suggests that the zebra finches' spatial decision of where to forage is shaped by the air temperature and the availability of water in this arid area. Drinking regularly helps to prevent overheating during the hottest hours of the day (Calder, 1964; Calder & King, 1963). Although the importance of water for thermoregulation is well known and documented (Calder, 1964; Tieleman & Williams, 2002; Zann, 1996), to our knowledge this is the first description of a spatial change in foraging activity in relation to water and induced by high temperature, based on the monitoring of individuals' movement at a fine temporal and spatial scale.

412 The importance of water and the physiological constraints of heat were further
413 supported by our observations of birds during the hottest periods of the day, and the hottest
414 days, when we encountered zebra finches sitting in small groups near the water. We found that
415 by the time air temperatures reached 35 °C, a significant proportion of birds were panting, in
416 line with previous studies (Schleucher, 1993; Zann, 1996), as well as wing spreading or fanning
417 (Eto, Withers, & Cooper, 2017; O'Connor et al., 2018; Tieleman & Williams, 1999). Above
418 41 °C individuals also exhibited two other behaviours, which we were unable to find any
419 reference to, in a heat dissipation context. Tail fanning, a behaviour previously observed in
420 breeding males during nest searching (Zann, 1996), was performed by both sexes a small
421 proportion of the time, but only at temperatures above 41 °C, suggesting it may be used as a
422 further method of either passive or cutaneous evaporative cooling (Gerson, Smith, Smit,
423 McKechnie, & Wolf, 2014), possibly by increasing airflow to the rump of the bird.
424 Furthermore, some individuals adopted an unusual position with the tail fanned and the wings
425 held partially spread out so that they were touching the tail, while the bird sat in a hunched-up
426 position, usually very low on its perch. This position may have acted to increase airflow to both
427 the tail and axillary regions at the same time. Moreover, it may have signified a level of heat
428 stress in individuals.
429 The second aspect on which our study provided new insight was in relation to the
430 temporal spread of foraging behaviour in relation to extremely hot conditions. While numerous
431 studies have found that the level of foraging is typically reduced in hot periods (Carmi-Winkler
432 et al., 1987; du Plessis et al., 2012; Edwards et al., 2015; Smit et al., 2013; Tieleman &
433 Williams, 2002), we have been able to examine this in the context of a far longer period of
434 behavioural monitoring. As expected, we found that individuals' foraging activity was
435 influenced by both temperature and time of day, but importantly, on the hottest days the
436 timetable of foraging activity was significantly different, with individuals deferring their

foraging activity until significantly later in the afternoon/evening. We believe that this is a sensible behavioural change to enable the birds to avoid foraging earlier in the day when it is hot, given that our feeders probably represented a fairly stable source of food which birds could rely on later in the day. The two peaks of activity predicted by optimal mass regulation theory (Houston, McNnamara, & Hutchinson, 1993) were confirmed in our data, as well as the extreme inactivity during the hottest hours of the day (1100–1600 hours, Fig. A2; Angiletta, Cooper, Schuler, & Boyles, 2010; McNamara, Houston, & Lima, 1994). Therefore, we are reasonably confident that the use of feeders reflects a natural foraging pattern for a passerine bird. In a previous study at the same site during the breeding season (a cooler period of the year) individuals frequented the feeders more constantly throughout the day, with some variation during different phases of the breeding cycle (Mariette et al., 2011). By contrast, a more bimodal distribution of foraging behaviour was found in captive zebra finches in unpredictable food availability conditions, without breeding activity or predation risk (Dall & Witter, 1998). During our study period very few breeding attempts were observed and there was no successful breeding, in line with recent findings showing that arid zone Australian birds typically do not breed in the summer (Duursma et al., 2017). According to theoretical foraging models (Houston et al., 1993), it seems likely that on the hottest days, individuals were refraining from foraging throughout most of the day until it became a little cooler, at which time they needed to forage more intensively to take on food before nightfall. Further studies are required to better investigate how food predictability can change foraging dynamics both during and outside the breeding period.

Our results suggest therefore that while there may be significant drops in foraging behaviour during hot conditions, individuals may significantly alter the timetable of foraging across the day. As such, previous studies that have determined the effect of extreme temperature on foraging activity (e.g. Carmi-Winkler et al., 1987; Edwards et al., 2015;

462 Goldstein, 1984; Ricklefs & Hainsworth, 1968), may have perhaps overestimated the extent to
463 which heat might affect an individual's intake across the whole day. Although we did not
464 examine food intake, our results may suggest that a short period of intense foraging later in the
465 day may, at least partially, provide the opportunity to make up lost foraging during a hot day.
466 The extent to which this is possible will of course depend on the extent to which the day cools
467 in the late afternoon and the foraging pattern of the species. For example, the efficiency of
468 foraging across the day may also covary with time for other reasons such as the depth or
469 availability of prey or the light levels (Fernandez-Juricic & Tran, 2007). We did not measure
470 the effect of these extreme heatwaves on the body condition or mass of our birds, and note
471 some of the previous studies have done so (du Plessis et al., 2012; Edwards et al., 2015). This
472 would be a very effective way of determining the short- to medium-term effects of hot
473 conditions on foraging and body condition.

474 Although we did not measure food intake in this study, it seems likely that the reduced
475 level of foraging activity would be coupled with a reduced food intake, because the birds are
476 always likely to be exposed to a high risk of predation while out foraging, and it is unlikely
477 that they would have increased the rate at which food was processed while at the feeders on
478 hot rather than cool days (i.e. we do not believe the foraging efficiency would change). It would
479 be useful to explore the relationship between air temperature and food intake directly, and
480 ideally account for variation in metabolic rate. However, until such work is done, if we assume
481 that all else is equal, then it seems likely that the reduced foraging activity during high
482 temperatures will constrain successful reproductive activity (when foraging demands on adult
483 birds are typically at their highest level), and potentially also prove physiologically costly if
484 adults are unable to meet their daily nutritional requirements. Again, it would be interesting to
485 examine the extent to which adults lose body condition during sustained periods of high air
486 temperatures and heatwaves in particularly (e.g. du Plessis et al., 2012; Edwards et al., 2015).

The negative relationship between high temperatures and foraging activity we have demonstrated could be interpreted as one cause of the low body size of zebra finches that were reared during hot conditions in the field (Andrew et al., 2018, 2017; Cunningham et al., 2013) and the avoidance of breeding in summer for arid species generally in Australia (Duursma et al., 2017).

Overall, our results highlight that hot conditions affect spatial, temporal and social patterns of foraging activity in this nonterritorial granivorous species and adds a level of insight into the way in which birds will respond to extreme heat events and to an increasingly hot climate. The effects that we demonstrated using our tracking system have potential downstream effects on body condition, physiology, life history and predation, all of which should be examined in future studies.

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Author Contributions

S.C.G., W.S. and C.F. developed the idea of this project; L.M. and C.F. collected the field data; C.F. conducted all the analysis and wrote the paper with contributions from all other authors.

Data Availability

The data sets analysed during the current study are available from the corresponding author on reasonable request.

Declaration of Interest

We have no competing interests.

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Figures Legends

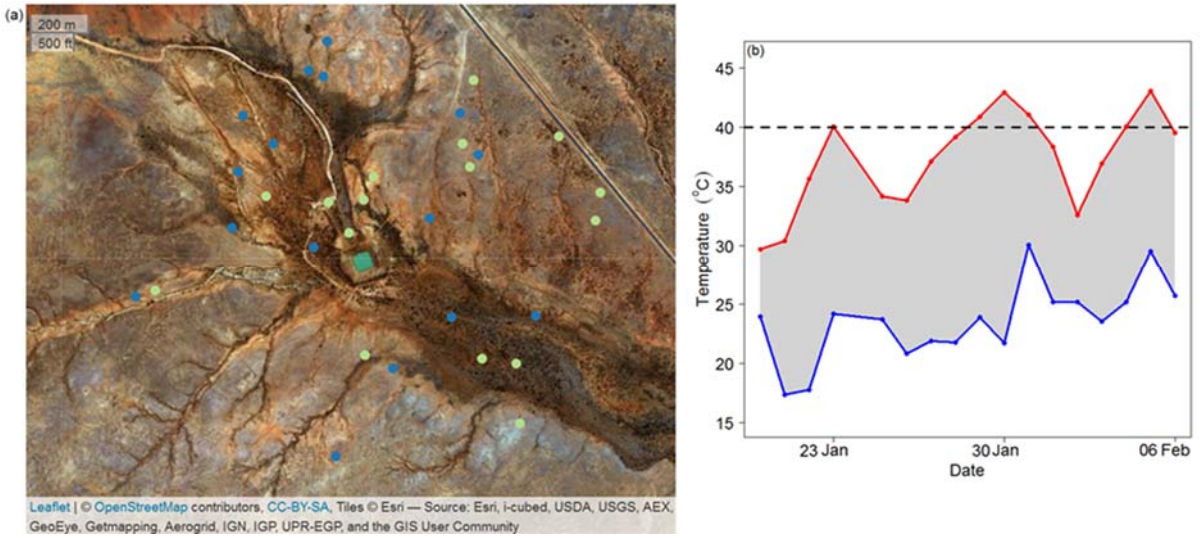


Figure 1 (a) Spatial distribution of the feeders of the first (green circles) and second trial (blue circles). The green square in the satellite map is the water dam. (b) Daily average minimum (blue) and maximum (red) air temperatures over the study period. The dashed line at 40 °C marks the threshold to identify the two heatwaves (as at least 2 days above the line).

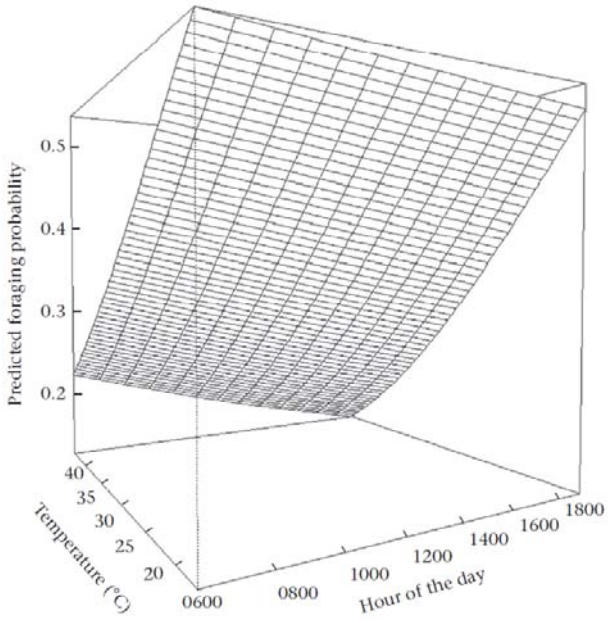
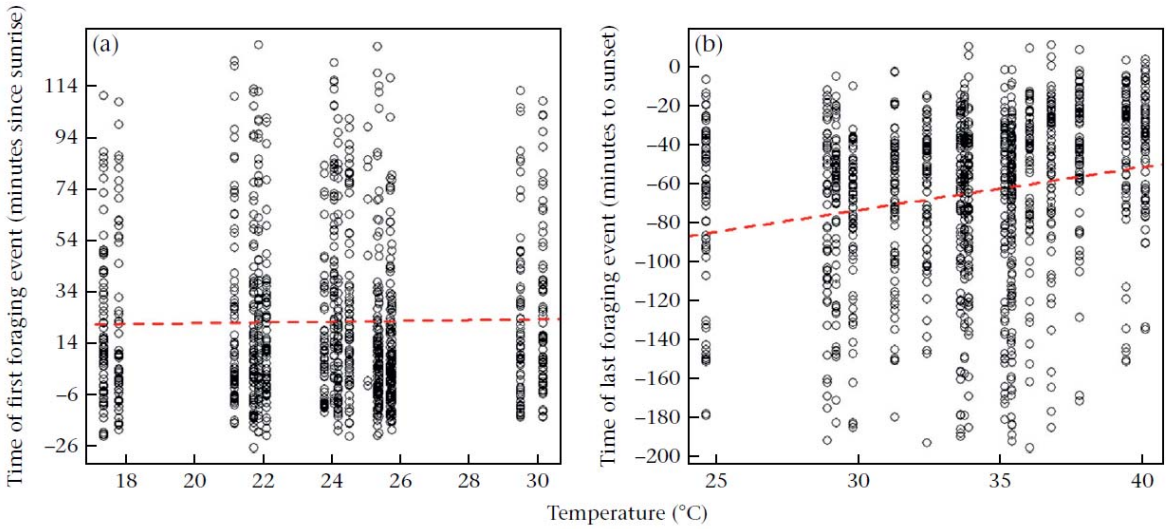
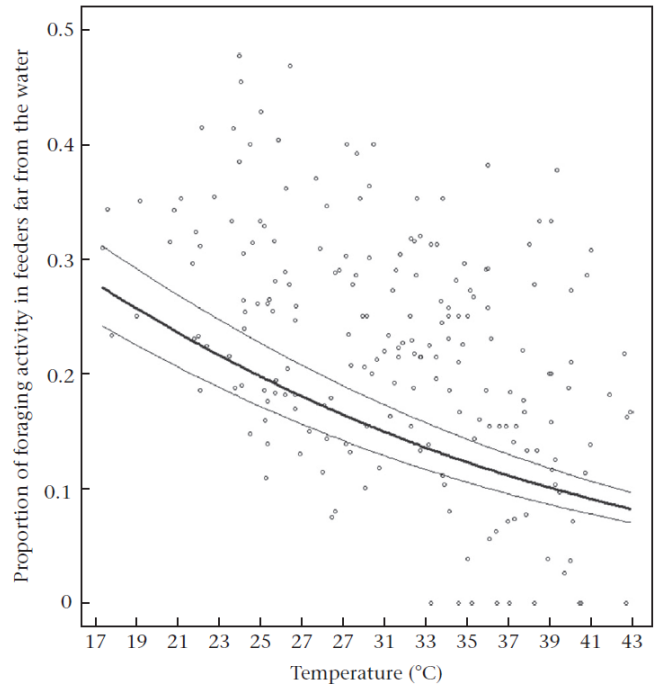


Figure 2 Predicted probability of foraging activity (as individuals' presence at the feeders) as a function of air temperature, hour of the day and their interaction.



670

671 **Figure 3** The zebra finches' (a) time of first feeding event (as minutes since sunrise) and (b)
672 time of last feeding event (as minutes to sunset) as a function of air temperature. Note that
673 negative values represent time before (a) sunrise and (b) sunset.



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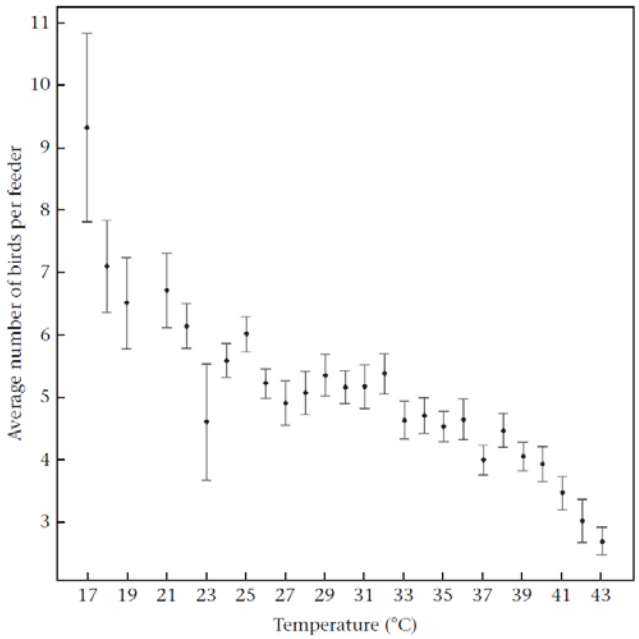
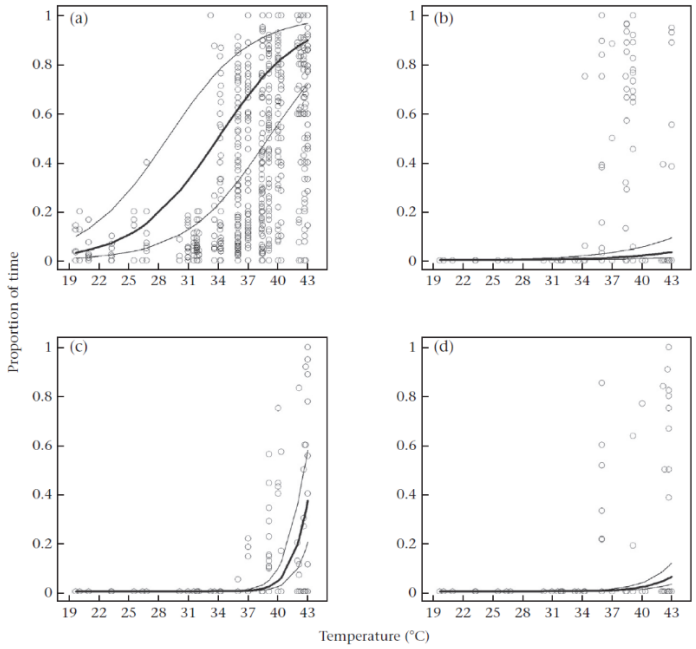
675 **Figure 4** Proportion of visits to the feeders located furthest from the water source in relation
676 to air temperature. The logistic curve and its interval of variation (95% confidence interval) are
677 shown.



678

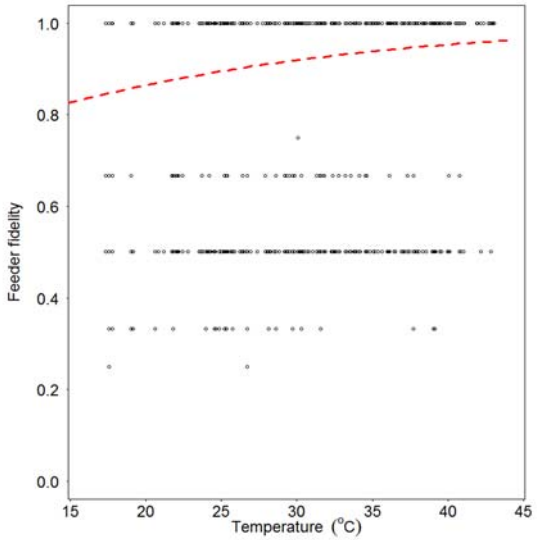
679 **Figure 5** Mean ± SE number of zebra finches per feeder within 15 min intervals in relation to
680 air temperature. Data are summarized to means and SEs per degree Celsius based on raw data
681 for illustrative purposes. Analyses were carried out on average air temperatures per hour (not
682 rounded to the next integer).



683

684 **Figure 6** Adult heat stress behaviours (as proportion of time) as a function of temperature. (a)
685 Bill kept open, (b) wings lifted away from body, (c) tail fanned and (d) spread out position.

686 The logistic curves with their intervals of variation (95% confidence interval) represent the
687 probability of showing the behaviour (based on presence/absence of each behaviour in every
688 observation) in relation to temperature. In (a) the likelihood of the behaviour 'bill kept open'
689 occurring is based on a model that does not include the interaction between hour of the day and
690 temperature, to facilitate comparison with the other graphs.



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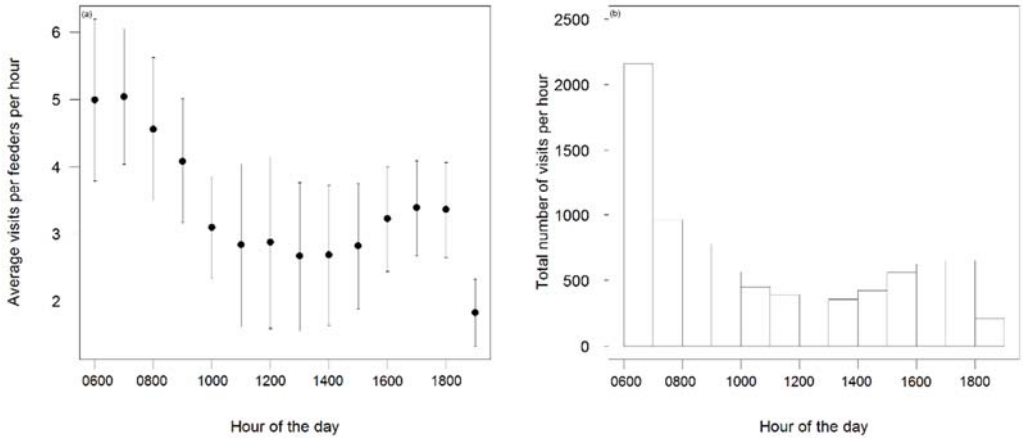
692 **Figure A1** Feeder fidelity, i.e. the proportion of visits of an individual to its most frequented
693 feeder per hour, as a function of air temperature. The red dashed line represents the model
694 predicted relationship.



695

696 **Figure A2** (a) Mean hourly number of visits to the feeders ± SD and (b) total number of visits
697 per hour.

698

699

700 **Table 1** Summary of all (G)LMMs

Response variable	Random term	*N*	Variance	Fixed effect	Estimate	SE	X^2 (*df*)	*P*
Air temperature (continuous)	Date	17	12.31	(Intercept)	20.35	1		
	(Residual)		9.35	Hour	0.91	0.04	282.6 (1)	**<0.001**
Foraging activity (binary)	ID	81	0.34	(Intercept)	0.89	0.26		
	Date	17	0.04	Temperature	-0.04	0.01		
				Hour	0.02	0.02		
				Temperature*Hour	-0.001	0	5.13 (1)	**0.02**
Foraging duration proxy (count)	ID	81	0.006	(Intercept)	0.5	0.05		
	Date	17	0.001	Temperature	-0.004	0.001	7.3 (1)	**0.007**
	Feeders	32	0.004	Hour	0.003	0.003	1.06 (1)	0.3
				Temperature*Hour	(<0.001)	(<0.001)	0.1 (1)	0.9

	ID	81	270.59	(Intercept)	18.76	17.7		
Time of first foraging	Date	17	88.64	Temperature at sunrise	0.15	0.73	0.04 (1)	0.83
event (continuous)	(Residual)		681.44					
	ID	81	463.88	(Intercept)	-140.5	17.7		
Time of last foraging	Date	17	53.49	Temperature at sunset	2.22	0.52	12.4 (1)	**<0.001**
event (continuous)	(Residual)		1170.04					
	ID	81	6.9	(Intercept)	535.2	2.04		
Distance of feeder	Date	17	0	Temperature	- <0.001	0.001	3161.7 (1)	**<0.001**
visited to water	Feeders	32	141.7	Hour	-(<0.001)	(<0.001)	0 (1)	1
(continuous)	(Residual)		0	Temperature*Hour	-(<0.001)	(<0.001)	0 (1)	1
	Date	17	0.03	(Intercept)	-0.01	0.17		
				Temperature	-0.06	0.01	32.64 (1)	**<0.001**

Proportion of visits to feeders furthest to dam (proportion)				Hour	0.04	0.01	11.15 (1)	**<0.001**
				Temperature*Hour	(-0.002)	-0.001	2.53 (1)	0.11
Feeder fidelity (proportion)	ID	81	0.27	(Intercept)	0.7	0.2		
	Date	17	0.12	Temperature	0.06	0.007	71.8(1)	**<0.001**
				Hour	(-0.02)	0.02	1.4 (1)	0.23
				Temperature*Hour	(-0.001)	(0.001)	0.7 (1)	0.4
Number of birds around each feeder in 15 min interval (count)	Unique 15 min period	914	0.14	(Intercept)	2.27	0.09		
	Feeders	32	0.07	Temperature	-0.03	0.002	124.07 (1)	**<0.001**
Bill open (binary)	Date (group)	19	0.9	(Intercept)	8.32	6.15		
				Duration	0.02	0.004	30.1 (1)	**<0.001**
				Temperature	-0.28	0.19		
				Hour	-1.43	0.5		

				Temperature*Hour	0.04	0.015	5.84 (1)	**0.004**
Wings away (binary)	Date (group)	19	5.56	(Intercept)	-19.73	7.27		
				Duration	0.03	0.006	26.14 (1)	**<0.001**
				Temperature	0.75	0.3	10.88 (1)	**0.013**
				Hour	-1.12	0.53	8.08 (1)	**0.03**
				Temperature*Hour	(-0.13)	0.14	1.57 (1)	0.21
Tail fanned (binary)	Date (group)	19	0.65	(Intercept)	-28.48	5.62		
				Duration	0.02	0.01	4.51	**0.03**
				Temperature	0.63	0.14	30.95 (1)	**<0.001**
				Hour	0.03	0.21	0.03 (1)	0.87
				Temperature*Hour	(-0.06)	0.11	0.37 (1)	0.54
Spread out position (binary)	Date (group)	19	1.2	(Intercept)	-23.68	5.83		
				Duration	0.02	0.01	5.37 (1)	**0.02**

Temperature	0.48	0.14	26.84 (1)	**<0.001**
Hour	(-0.14)	-0.3	0.02 (1)	0.64
Temperature*Hour	(-0.03)	-0.08	0.13 (1)	0.72

Response variables, random terms, sample size (*N*) and variance are specified for each model. Value of fixed effects (estimated) and SEs are estimates for the variables in a minimal adequate model; values in parentheses represent coefficients and SEs from the model before the term was dropped. Significant *P* values are highlighted in bold.